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Effects of alien plant management, fire and soil chemistry on selected soil microbial populations in the Table Mountain National Park, South Africa

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This pilot study examined changes in soil chemistry and microbial population sizes following the extensive wildfires in 2000 on the Cape Peninsula. The effects of standing alien plants and stacks of mechanically-cleared alien plant material on selected post-fire microbial populations and their recovery were investigated. These were compared to burnt fynbos and the burnt cleared areas surrounding wildfire burnt stacks. Microbial population sizes and chemical changes were also monitored in unburnt fynbos and dense unburnt stands of invasive alien plants. Differences in soil chemistry and microbial population sizes occurred in the samples taken from the various post-fire environments while marked seasonal changes were also apparent. Microbial population sizes were linked to pre-fire vegetation characteristics, fire intensity, the management of alien plants, soil chemical changes and seasonal influences. High volumes of woody alien plant biomass impacted on post wildfire microbial population sizes during summer. During winter, however, microbial population sizes were primarily influenced by soil texture and nutrient composition.

Introduction

Fire is considered to be the chief perturbation in many Mediterranean-type ecosystems and is important for the combustion and mineralisation of slowly decomposing litter (Groves 1983, Mitchell 1983). Decomposition as a biological mineralisation process operating between fires may also be extremely significant (Rundel 1983). Soil-borne micro-organisms play major roles in the decomposition and mineralisation of organic compounds and in the transformation of inorganic nutrients in ecosystems, making them available to higher plants (Alexander 1977, Paul and Clark 1996). Soil micro-organisms also play vital roles in many physiological processes and are crucial to a number of biochemical reactions essential to plant survival (Tan 1994, Paul and Clark 1996). Carbon and nitrogen cycling are among the most important arenas of microbial decomposition and mineralisation (Tan 1994).

Fire and fire temperatures also influence the nutrient status of the soil in fynbos (Rundel 1983, Brown and Mitchell 1986, Van Reenen *et al.* 1992) and in a variety of other ecosystems (De Bano *et al.* 1979, Arianoutsou and Margaris 1981, Pietikainen and Fritze 1995, Dumontet *et al*. 1996, Hernandez *et al.* 1997, Grogan *et al.* 2000, Jensen *et al*. 2001). High temperatures increase volatilisation from the canopy and litter, reducing fluxes to the soil compartments (Rundel 1983). This may influence post-fire microbial populations, their development and activity (Brown and Mitchell 1986). Burn intensities in the January 2000 fires in the Table Mountain National Park's Silvermine area were extremely high because of large volumes of well-cured fuels and hot, dry windy conditions (Euston-Brown 2000, Scott *et al.* 2000). Those areas densely invaded by woody alien plants had exceptionally high fuel loads and were consequently subjected to the hottest fires (Scott *et al.* 2000).

Current fynbos management consists largely of controlling and applying fire, and combatting invasions of woody weed species (Van Wilgen and Richardson 1985). Approximately a quarter of the total area burned on the Cape Peninsula was cleared mechanically of woody alien plants over the two years before the fire (Scott *et al.* 2000). In these areas, the cleared vegetation was pulled into stacks. During the fire these stacks burnt at highly elevated temperatures because of high concentrations of dead dry fuel and they consequently formed so-called heat scars on the landscape (Breytenbach 1989, Holmes 1989, Macdonald *et al*. 1989, Euston-Brown 2000, Scott *et al.* 2000).

Some studies have documented the effects of fire on soil micro-organisms and their activities in the soil of kwongan in Australia (Pattinson *et al.* 1999), chaparral in California (Dunn *et al.* 1979, 1985), Douglas Fir in Oregon (Wright and Bollen 1961), prairie in Manhattan (Ajwa *et al*. 1999) and phrygana in Greece (Arianoutsou-Faraggitaki and Margaris 1982). Van Reenen *et al.* (1992) tested this association in fynbos. To date, no study has yet investigated possible links between fire, soil chemistry and soil microbial populations in

burnt standing alien, burnt stacked alien slash, burnt mechanically-cleared areas (surrounding scars) and in burnt fynbos. This is a pioneering study to investigate the post-fire effects of alien vegetation and management on the sizes of selected soil microbial populations.

Materials and Methods

Sample collection

On 1 November 2000 (summer, 10 months after the fire), soil samples were collected from six habitat types: burnt standing alien (S 34.10251; E 18.40415), burnt fynbos (S 34.10338; E 18.40458), unburnt fynbos (S 34.10489; E 18.40455), unburnt standing alien (S 34.10506; E 18.40305), burnt stacked alien slash and burnt cleared areas surrounding stacks (S 34.10043; E 18.42422). In the figures and tables these habitat typese are referred to as follows: 'burnt alien', 'burnt fynbos', 'unburnt fynbos', 'unburnt alien', 'heatscar' (resulting from burning stacked alien slash) and 'burnt cleared'. An auger (0.075m diameter) was used to sample soil to a depth of 0.10m. The samples included any surface organic material which may have been present. Five independent samples of approximately 0.001767m^3 were taken from each habitat and bulked. Similar sampling was repeated on 15 March 2001 (autumn), 4 July 2001 (winter) and 7 September 2001 (spring) to assess seasonal changes.

Soil analyses

Soil chemical and physical analyses were conducted by Bemlab^{BK} (AECI Building W21, De Beers Street, Somerset West). Particle size distribution was determined using a hydrometer method (Van der Watt 1966). Exchangeable cations (Ca, Mg, K and Na) were determined in a 1M ammonium acetate extract (Doll and Lucas 1973). The trace elements Mn, Cu and Zn were determined in a diammonium EDTA extract (Beyers and Coetzer 1971). A hot water extract was used to quantify B (Anonymous 1974). Total nitrogen was determined by digestion in a LECO FP-528 nitrogen analyser, while organic carbon was determined with the Walkley-Black method (Nelson and Sommers 1982). Total organic matter was then calculated by multiplying organic carbon content by 1.72 (Baldock and Skjemstad 1999). Ammonium (NH_4) and nitrate (NO_3) were determined in a 1M KCl extract (Bremner 1965). Soil pH was determined in 1M KCl (McClean 1982). Cation exchange capacity (CEC) was determined at pH 7 by saturation with 0.2M ammonium acetate, whereafter the NH_4 was displaced with K_2SO_4 and determined by Kjeldahl distillation (Peech 1965).

Microbial analyses

Selected soil microbial populations in the bulked samples were enumerated using standard microbial plate count methods. The soil dilution plate technique was used in combination with a series of selective and non-selective isolation media and all plates were incubated at 22°C while they were monitored for the appearance of microbial colonies. Total heterotrophic counts on tryptone soy agar (TSA, Biolab™ distributed by Merck Chemicals (Pty) Ltd, Cape Town) were obtained after five days of incubation. On all the other media, the microbial colonies were enumerated after seven days of incubation. Actinomycetes were enumerated on sodium caseinate agar. This medium (pH 6.7) consisted of 0.2gl^{-1} sodium caseinate, 0.5gl^{-1} K_2HPO_4, 0.2gl^{-1} $MgSO_4$, 0.01gl^{-1} $FeCl_3$ and 15.0gl^{-1} agar. Malt extract agar (MEA, Biolab™) supplemented with an anti-bacterial agent such as 0.5gl^{-1} streptomycin sulphate is a relatively non-selective fungal isolation medium (Atlas 1995) and was used to enumerate a wide diversity of fungi in the soil, while thymine-mineral-vitamin agar (TMV) was used since it selects for physiologically-related ascomycetous and basidiomycetous soil yeasts and simultaneously prevents over-growth of filamentous fungi (Cornelissen *et al.* 2003). Hymenomycetous fungi were enumerated using a benomyl-dichloran-streptomycin (BDS) medium containing 15.0gl^{-1} malt extract, antifungal agents (0.002gl^{-1} benomyl, 0.002gl^{-1} dichloran, 0.05gl^{-1} phenol), 0.1gl^{-1} streptomycin sulphate and 15gl^{-1} agar (Worrall 1991). Mucor isolation medium A was used to enumerate mucoralean fungi (Strauss *et al.* 2000).

Statistical analyses

The Fire Severity Index of Euston-Brown (2000) was adapted to include subjective assessments of pre-fire climatic conditions, weather conditions during the fire, pre-fire fuel loads and packing along a sliding scale of increasing influence. Values obtained from this adapted fire severity index were included as abiotic environmental variables in the analyses.

Maximum Harmonic (weighted Spearman) correlations (r_w) of the distributions of micro-organisms with sets of environmental variables were calculated using the BIOENV application of the software program PRIMER (Clarke and Warwick 1994). When viewing the results it must be considered that environmental variable sets portrayed in Tables 3–8 are a consequence of optimal selection by the BIOENV procedure and result from repeated runs of the analysis. Repeated analyses were necessitated since the application can only cope with a maximum of 10 000 combinations. Repetition does, however, result in the possibility of Type 1 errors. Furthermore the ranks are not mutually independent variables and are based on a large number of strongly interdependent similarity calculations. It is therefore erroneous to refer r_w to standard statistical tables to assess significance. This does not, however, compromise the use of r_w as an index of agreement between matrices since any variables featuring arbitrarily or marginally in one run would be unlikely to do so in further repetitions. In conclusion, BIOENV is an exploratory, rather than an inferential, statis-tical tool. Its use is to rank various variable combinations and to compare these clusters against each other in order to produce an optimal cluster of abiotic variables best explai-ning patterns in measured biotic data (Clarke and Warwick 1994).

Results

Soil chemical changes

Differences in soil chemical status of the samples analysed were observed between those obtained from natural and transformed fynbos habitats while differences between seasons were also apparent. Only the most important and obvious changes observed are summarised here.

Soil sample pH dropped markedly while CEC rose in the period from November 2000 to March 2001, in the absence of large rainfall events (Figures 1 and 2). The drop in pH in March 2001 corresponded with a sharp increase in NO_3 and NH_4 levels (Figures 3 and 4). Potassium levels remained relatively constant in unburnt fynbos and burnt cleared area samples but fluctuated in all the other treatments (Figure 5). In November 2000 and March 2001, K levels were higher in burnt fynbos, burnt standing aliens and burnt stacked areas than in unburnt fynbos, unburnt standing aliens and burnt cleared areas respectively (Figure 5). Phosphorus levels were consistently higher in burnt than in unburnt areas, except in September 2001, when unburnt and burnt fynbos had similar levels and burnt stack sites had low levels (Figure 6). The changing amounts of P in the soil showed some correlation with plate counts of mucoralean fungi in November 2000, soil yeasts in March 2001 (MEA) and with total heterotrophic microbial counts (TSA) in September 2001. The contribution of Mg to the total CEC of the soil samples (Mg %) gradually increased from November 2000 to September 2001 (Figure 7).

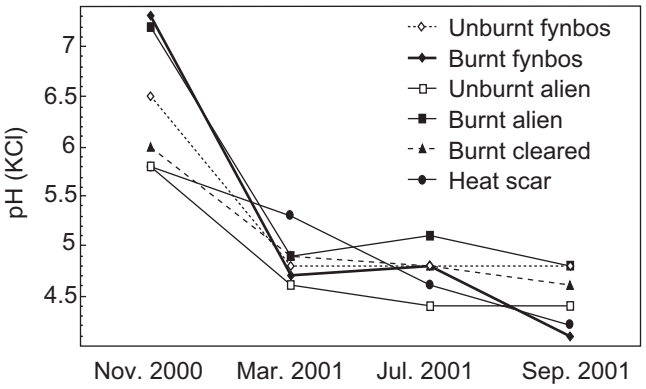

Figure 1: Seasonal changes in soil pH (KCl) in various natural and transformed fynbos habitats

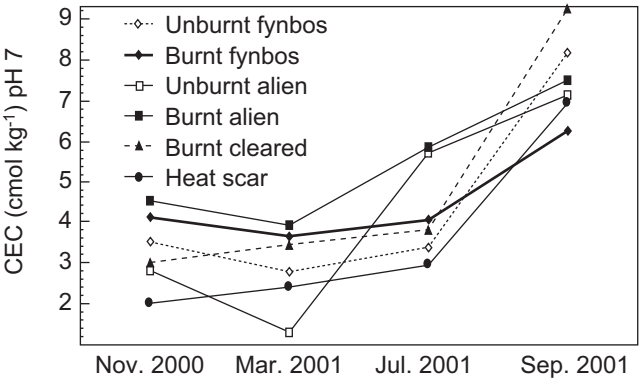

Figure 2: Seasonal changes in soil cation exchange capacity (CEC) in various natural and transformed fynbos habitats

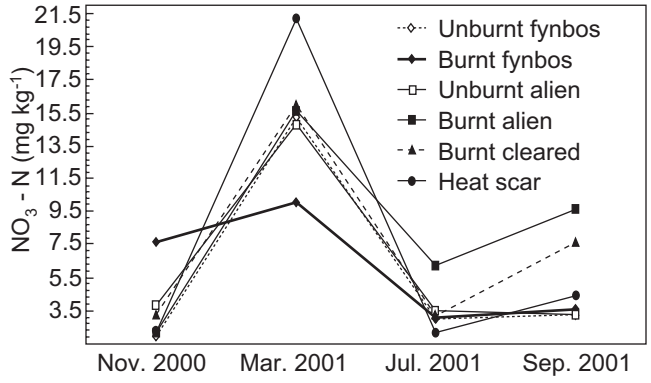

Figure 3: Seasonal changes in soil nitrate (NO_3) levels in various natural and transformed fynbos habitats

Soil fungi

Populations of soil yeasts in the samples analysed showed clear differences between sites in the November 2000 and March 2001 assays (Table 1). These distributions showed maximum correlation with soil texture and fire intensity in November. However, this changed to maximum correlation with a set of macronutrients and fire intensity by March 2001 (Table 3). By July 2001, soil yeast populations had grown, particularly in the unburnt standing alien area. However, burnt sites still had lower counts, except for burnt stacked areas where counts were higher than for burnt cleared areas. Maximum correlations were with soil texture, pH and Mg and Na levels. By September 2001, populations of soil yeasts were similar except for unburnt fynbos, which exhibited larger population sizes. Again, maximum correlation in this assay was with soil texture and Mg and Na contents, but not with soil pH.

While counts of mucoralean fungi in November 2000 showed differences between burnt and unburnt areas (Table 1), maximum correlation was not with fire intensity, but with soil texture and the macronutrients P and K (Table 4). The distribution in autumn (March 2001) was correlated with a different set of nutrients viz. Na, Ca, NO_3, as well as resistance, % fine sand, % stone and fire intensity. While populations had increased by July 2001, the counts showed poor correlation with environmental variables measured. Populations were unstable in September 2001 with large increases in burnt standing alien areas and a total collapse in burnt stacked sites. Environmental variables showing maximum correlation with these counts were soil texture, pH, Ca and fire intensity (Table 4).

In November 2000, some hymenomycetaceous fungal populations showed reduced population sizes (Table 1). Observed trends indicated reductions in burnt standing aliens and in burnt stack populations. However, there were no observed differences between burnt fynbos, unburnt fynbos and burnt cleared area samples. The environmental variables best explaining this distribution included soil texture and Mg levels (Table 5). Nutritional variables became more important by March 2001 when counts were best correlated with CEC, Ca content as well as % stone and % coarse sand. All the post-fire habitats also had higher counts in March than unburnt habitats, those habitats subjected to the most severe burns, burnt standing aliens and wildfire burnt stacks having the highest counts. Differences between the means (in July 2001) are best explained by the contribution made by Mg to the CEC, %

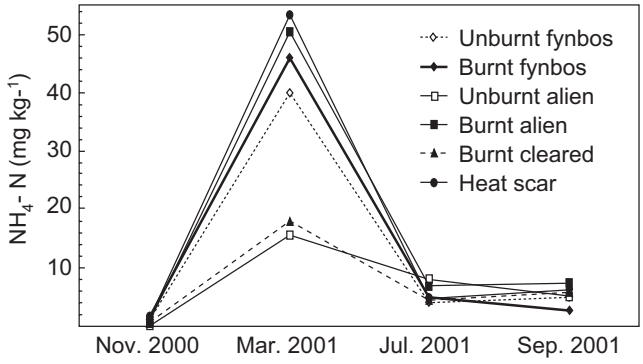

Figure 4: Seasonal changes in soil ammonium (NH_4) levels in various natural and transformed fynbos habitats

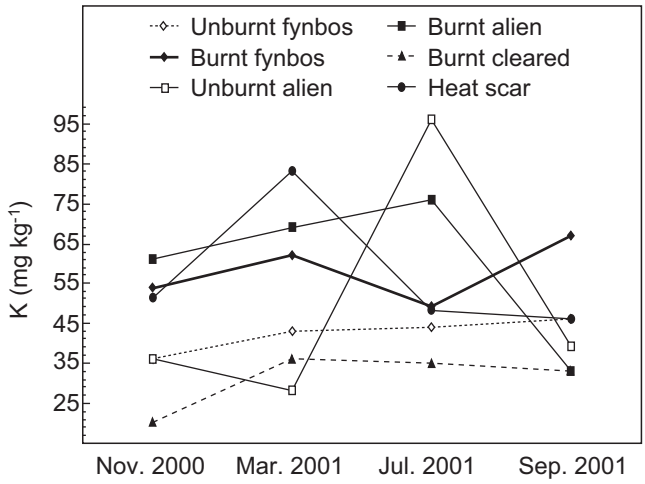

Figure 5: Seasonal changes in soil potassium (K) in various natural and transformed fynbos habitats

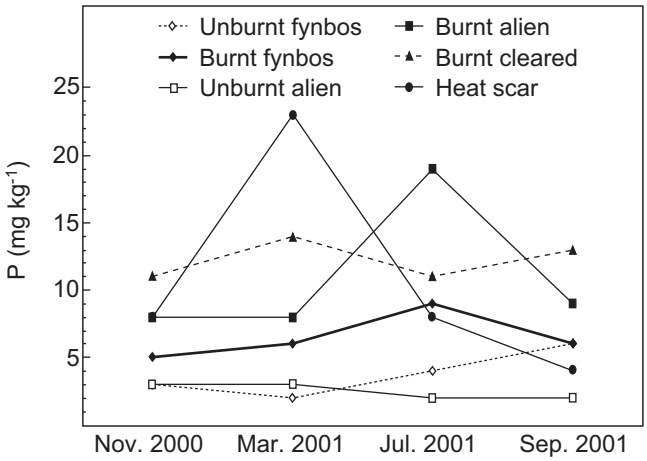

Figure 6: Seasonal changes in soil phosphorus (P) in various natural and transformed fynbos habitats

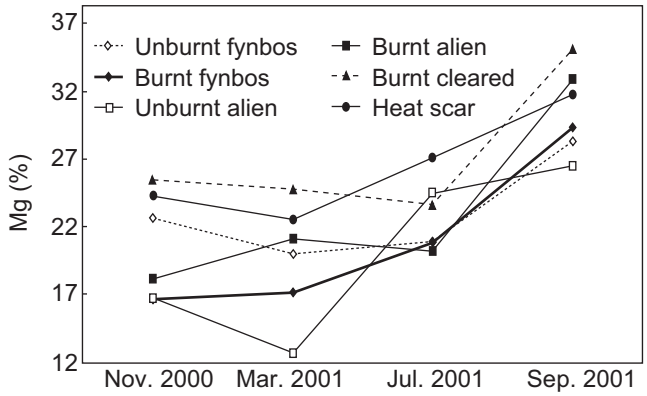

Figure 7: Seasonal changes in percentage magnesium (Mg) of the total exchangeable cations (cmol/kg) of the soil in various natural and transformed fynbos habitats

medium sand, pH and NO_3 (Table 5). September 2001 was marked by the disappearance of all traces of hymeno- mycetes in the heat scar samples, the other habitats having similar population sizes. This pattern is best explained by differences in pH, % stone and % clay between the studied habitats.

Populations of total fungi (as enumerated on MEA medium) in November 2000 were higher in soils under burnt stacks than in the burnt cleared areas (Table 1). By March 2001, however, total populations of fungi were similar across all the treatments. In July 2001, burnt standing aliens had the highest populations of total fungi. In September 2001, unburnt and burnt standing alien habitats had the highest totals. Only in September was the distribution of total fungi (MEA) adequately explained by strong correlation with environmental variables measured viz. % clay, % stone, % fine sand as well as resistance and P and N levels (Table 6).

Soil actinomycetes and heterotrophic organisms (bacteria)

Actinomycete counts on sodium caseinate agar in November 2000 were highest in burnt and unburnt fynbos habitats and higher in burnt aliens and burnt stacked soils than unburnt aliens and burnt cleared areas respectively (Table 2). Actinomycete populations at this stage showed maximum correlation with a combination of soil texture and nutrients: CEC, resistance and Na (Table 7). By March 2001, the actinomycete counts in unburnt fynbos had shown larger increases in population size than in any of the other areas. This distribution was maximally correlated with soil texture (silt, medium sand, coarse sand and stone) and not with the soil nutrients measured. By July, all areas (except for unburnt fynbos) had shown large increases in population size. This coincided with the advent of cool, wet winter weather. The largest increases occurred in non-fynbos areas. There was, however, poor correlation between distribution patterns in this assay and the measured environmental variables. By September 2001, all populations had declined and burnt fynbos soils retained the highest actinomycete counts. This distribution showed maximum correlation with pH, Ca, C, % clay and CEC (Table 7).

Total heterotrophic counts (on TSA medium) in November 2000 revealed little difference between the sites; only the wildfire burnt stacks and the burnt cleared areas surrounding

Table 1: Seasonal changes in the number of fungal colony-forming units per gram soil counted on selected isolation media (n = 3). Figures in parenthesis indicate standard errors of the means

	Season			
	Summer 2000	Autumn 2001	Winter 2001	Spring 2001
Soil yeasts				
Unburnt fynbos	9.5 x 10^3 (218.58)	1.1 x 10^4 (705.53)	2.3 x 10^4 (1 733.33)	2.3 x 10^4 (961.48)
Burnt fynbos	2.8 x 10^3 (120.19)	6 x 10^3 (611.01)	1.3 x 10^4 (533.33)	1.4 x 10^4 (811.04)
Unburnt alien	9.5 x 10^3 (437.16)	1.7 x 10^4 (1 919.49)	6.4 x 10^4 (520.68)	1.3 x 10^4 (961.48)
Burnt alien	500.00 (57.74)	700.00 (57.74)	2.1 x 10^4 (480.74)	1.5 x 10^4 (692.82)
Burnt cleared	7.2 x 10^3 (560.75)	3.7 x 10^3 (33.33)	3.1 x 10^4 (1 866.67)	1.2 x 10^4 (480.74)
Heat scar	266.67 (66.67)	733.33 (88.19)	4.4 x 10^4 (1 733.33)	1.1 x 10^4 (352.77)
Mucoralean fungi				
Unburnt fynbos	6 x 10^3 (1 x 10^3)	1.2 x 10^3 (258.20)	8.3 x 10^3 (1 763.83)	4 x 10^3 (577.35)
Burnt fynbos	1 x 10^3 (577.35)	1.4 x 10^3 (316.23)	6.3 x 10^3 (4 333.33)	2.3 x 10^3 (1 333.33)
Unburnt alien	5 x 10^3 (1 527.53)	4 x 10^3 (1 354.01)	1.5 x 10^4 (2 333.33)	8.7 x 10^3 (1 452.97)
Burnt alien	666.67 (333.33)	200.00 (200.00)	2 x 10^4 (9 018.50)	5.9 x 10^4 (4 910.31)
Burnt cleared	4 x 10^3 (1 527.53)	1.8 x 10^3 (258.20)	1.4 x 10^4 (1 452.97)	1.8 x 10^4 (1 452.97)
Heat scar	0.00 (0.00)	200.00 (200.00)	6.7 x 10^3 (5 174.72)	0.00 (0.00)
Hymenomycetous fungi				
Unburnt fynbos	7.7 x 10^3 (2 848.00)	2 x 10^3 (1 000.00)	1.2 x 10^4 (333.33)	1.2 x 10^4 (1 201.85)
Burnt fynbos	7.7 x 10^3 (1 201.85)	7.7 x 10^3 (1 452.97)	1.3 x 10^4 (881.92)	1.5 x 10^4 (2 728.45)
Unburnt alien	7 x 10^3 (1 154.70)	333.33 (333.33)	1.6 x 10^4 (3 929.94)	1.5 x 10^4 (2 027.59)
Burnt alien	2.3 x 10^3 (1 201.85)	1.3 x 10^4 (2 645.75)	1.7 x 10^3 (881.92)	1.7 x 10^4 (1 333.33)
Burnt cleared	1 x 10^4 (666.67)	6 x 10^3 (1 154.70)	1.5 x 10^4 (577.35)	1.3 x 10^4 (2 516.61)
Heat scar	3.3 x 10^3 (333.33)	1.2 x 10^4 (1 000.00)	1.8 x 10^4 (666.67)	0.00 (0.00)
Total fungi (as enumerated on MEA)				
Unburnt fynbos	1.7 x 10^5 (2.6 x 10^4)	1 x 10^5 (2.7 x 10^4)	1.4 x 10^5 (1.5 x 10^4)	1.8 x 10^5 (4.5 x 10^4)
Burnt fynbos	1.9 x 10^5 (4.9 x 10^4)	7 x 10^4 (1.5 x 10^4)	1.5 x 10^5 (1.7 x 10^4)	1.7 x 10^5 (3 x 10^4)
Unburnt alien	8.7 x 10^4 (6.6 x 10^3)	9 x 10^4 (2 x 10^4)	1.2 x 10^5 (3.3 x 10^4)	3 x 10^5 (8.8 x 10^3)
Burnt alien	1.9 x 10^5 (3.5 x 10^4)	1.3 x 10^5 (5.8 x 10^3)	6.5 x 10^5 (8.8 x 10^4)	2.9 x 10^5 (2 x 10^4)
Burnt cleared	1.2 x 10^5 (8.8 x 10^3)	1.4 x 10^5 (1.5 x 10^4)	2.7 x 10^5 (5 x 10^4)	2 x 10^5 (3.7 x 10^4)
Heat scar	3.3 x 10^5 (1.5 x 10^4)	9 x 10^4 (2 x 10^4)	1.9 x 10^5 (6.7 x 10^4)	1.3 x 10^5 (5.8 x 10^3)

Table 2: Seasonal changes in the number of microbial colony-forming units per gram soil counted on selected isolation media (n = 3). Figures in parenthesis indicate standard errors of the means (actinomycetes and heterotrophic microbes)

	Season			
	Summer 2000	Autumn 2001	Winter 2001	Spring 2001
Soil actinomycetes				
Unburnt fynbos	7.4 x 10^5 (2 x 10^4)	9.5 x 10^6 (3 x 10^5)	4.3 x 10^6 (2.4 x 10^5)	3.8 x 10^5 (1.7 x 10^4)
Burnt fynbos	7.9 x 10^5 (2.3 x 10^4)	1.1 x 10^6 (5.8 x 10^4)	4.7 x 10^6 (1.5 x 10^5)	9.9 x 10^5 (3.2 x 10^4)
Unburnt alien	4.4 x 10^5 (2.6 x 10^4)	7 x 10^5 (1 x 10^5)	5.2 x 10^6 (2.2 x 10^4)	6.5 x 10^5 (4.3 x 10^4)
Burnt alien	6.9 x 10^5 (2.7 x 10^4)	1.4 x 10^6 (1.2 x 10^5)	7.6 x 10^6 (4.1 x 10^5)	3.8 x 10^5 (3.8 x 10^4)
Burnt cleared	2.4 x 10^5 (1.5 x 10^4)	2.8 x 10^6 (1.5 x 10^5)	8.3 x 10^6 (4.4 x 10^5)	5.2 x 10^5 (5.5 x 10^4)
Heat scar	6.2 x 10^5 (3.1 x 10^4)	1.3 x 10^6 (3.3 x 10^4)	9.6 x 10^5 (8.7 x 10^5)	2.3 x 10^5 (1.5 x 10^4)
Total heterotrophic microbial counts on TSA				
Unburnt fynbos	8.3 x 10^5 (8.8 x 10^4)	1 x 10^7 (3.7 x 10^5)	7.3 x 10^5 (6.7 x 10^4)	1.2 x 10^6 (2.1 x 10^5)
Burnt fynbos	1.2 x 10^6 (1.7 x 10^5)	1.2 x 10^6 (2.5 x 10^5)	1.2 x 10^6 (1.2 x 10^5)	1.2 x 10^6 (2.3 x 10^5)
Unburnt alien	8.3 x 10^5 (1.8 x 10^5)	3.3 x 10^5 (3.3 x 10^4)	1.1 x 10^6 (1.8 x 10^5)	6.3 x 10^5 (1.9 x 10^5)
Burnt alien	6.3 x 10^5 (8.8 x 10^4)	7.7 x 10^5 (2.4 x 10^5)	9.7 x 10^5 (1.2 x 10^5)	1.5 x 10^6 (2.3 x 10^5)
Burnt cleared	5 x 10^5 (1.2 x 10^5)	1.2 x 10^6 (3.3 x 10^4)	1 x 10^6 (8.8 x 10^4)	1.2 x 10^6 (1.7 x 10^5)
Heat scar	1.3 x 10^6 (8.8 x 10^4)	4.3 x 10^5 (3.3 x 10^4)	7.3 x 10^6 (3.6 x 10^5)	3.3 x 10^5 (6.7 x 10^4)

them differed, with stack counts higher than cleared area counts (Table 2). The distribution of total heterotrophic organisms in this assay showed some correlation with the contribution made by Na to CEC, pH and soil texture. Unburnt fynbos exhibited by far the highest total heterotrophic counts in March 2001 and the distribution's maximum correlation with environmental variables was again with soil texture and pH but now also included CEC. July 2001 showed a complete turnaround, with wildfire burnt stack soils having by far the highest counts of heterotrophic organisms on TSA medium. Nonetheless, the environmental variables best explaining the observed distribution were clay and the levels of C, Mg and exchangeable Ca. Considerable variation in total heterotrophic counts was evident in September 2001, although total plate counts from stacked area soils were the lowest at that time. The environmental variables showing maximum correlation with this distribution of means were % stone and P level (Table 8).

Table 3: Sets of environmental variables showing maximum harmonic (weighted Spearman) correlation (r_w) with the distributions of soil yeasts in each of four assays

Summer 2000	Autumn 2001	Winter 2001	Spring 2001
Silt %	Stone %	Silt %	Coarse sand %
Fine sand %	P (mg/kg) log (x)	Mg %	Mg (cmol/kg) log (x)
	K (mg/kg) log (x)	Clay %	Clay %
	Na (cmol/kg) log (x)	Na %	Na (cmol/kg) log (x)
	NO_3 (N) log (x)	pH (KCl) log (x)	Medium sand %
Fire intensity	Fire intensity		
r_w:0.812	r_w:0.872	r_w:0.798	r_w:0.834

Table 4: Sets of environmental variables showing maximum harmonic (weighted Spearman) correlation (r_w) with the distributions of mucoralean fungi in each of four assays

Summer 2000	Autumn 2001	Winter 2001	Spring 2001
Clay %	Fine sand %	Fine sand %	Coarse sand %
Silt %	Resistance *log (x)*	Resistance *log (x)*	H (cmol/kg) *log (x)*
Fine sand %	Stone %	Medium sand %	Stone %
P (mg/kg) *log (x)*	Na (cmol/kg) *log (x)*	Mg (cmol/kg) *log (x)*	
K (mg/kg) *log (x)*	Ca (cmol/kg) *log (x)*	NH_4 (N) *log (x)*	Ca (cmol/kg) *log (x)*
	NO_3 (N) *log (x)*	CEC *log (x)*	
	Fire intensity		Fire intensity
r_w:0.927	r_w:0.877	r_w:0.555	r_w:0.868

Table 5: Sets of environmental variables showing maximum harmonic (weighted Spearman) correlation (r_w) with the distributions of hymenomycetous fungi in each of four assays

Summer 2000	Autumn 2001	Winter 2001	Spring 2001
Mg %	T (cmol/kg) *log (x)*	Mg %	H (cmol/kg) *log (x)*
Clay %	Stone %	Medium sand %	Clay %
Silt %	Ca (cmol/kg) *log (x)*	pH (KCl)	Stone %
Coarse sand %	Coarse sand %	NO_3 (N) *log (x)*	
r_w:0.783	r_w:0.989	r_w:0.836	r_w:0.883

Discussion

Previously, it was found that increases of soil microbial respiratory activity as well as fungal and bacterial numbers and biomass occur in fynbos during the first post-fire rainy season after initial declines prior to the rain (Van Reenen *et al.* 1992). During these studies microbes were enumerated on a non-selective medium, so that the response of specific culturable microbial populations to the fire could not be determined. We have found that different culturable microbial populations responded differently to fire and subsequent chemical changes in the soil.

Soil chemical changes

It seems reasonable to speculate that the pH drop in Autumn 2001 corresponded with a sharp rise in NO_3 and NH_4 levels. This possibly resulted from the activities of nitrifying and denitrifying bacteria. The increases in NO_3 and NH_4 levels also corresponded with increased population sizes of actinomycetes and other heterotrophic micro-organisms capable of growth on TSA. Trends indicated possible influences of burning, plant cover, biomass and associated fire intensity on K levels in the soil during summer and autumn. In these assays (November 2000 and March 2001), wildfire burnt stacks (heat scars), burnt standing aliens and burnt fynbos treatments exhibited higher K levels than unburnt treatments (Figure 5). Wildfire burnt stacks also had higher K levels than the immediately adjacent burnt cleared areas. Potassium was also one of the environmental determinants of the distribution of soil yeasts in autumn. However, with the advent of winter (July 2001), the influence of burning, plant cover, biomass and fire intensity on K levels was no longer apparent. Winter was also the time of maximum fungal growth, and K showed no correlation with fungi or heterotrophic micro-organisms growing on TSA during this period.

Soil fungi

A correlation of soil yeast population sizes with environmental variables indicates prolonged effects of fire and fire intensity (at least 13.5 months). Furthermore, macronutrient availability during autumn appears to be an important determinant of soil yeast population sizes. Some recovery of soil yeast populations coincided with the onset of cooler winter weather and increased rainfall (July 2001). Macro-

Table 6: Sets of environmental variables showing maximum harmonic (weighted Spearman) correlation (r_w) with the distributions of total fungi enumerated on MEA in each of four assays

Summer 2000	Autumn 2001	Winter 2001	Spring 2001
Fine sand %	Clay %	Fine sand %	Clay %
Resistance *log (x)*	Silt %	N %	Resistance *log (x)*
Stone %	H (cmol/kg) *log (x)*	Fire intensity	Stone %
K (mg/kg) *log (x)*	NO_3 (N) *log (x)*	NO_3 (N) *log (x)*	Fine sand %
C %			P (mg/kg) *log (x)*
			N %
r_w:0.662	r_w:0.560	r_w:0.771	r_w:0.856

Table 7: Sets of environmental variables showing maximum harmonic (weighted Spearman) correlation (r_w) with the distributions of actinomycetes in each of four assays

Summer 2000	Autumn 2001	Winter 2001	Spring 2001
Clay %	Medium sand %	Mg %	H (cmol/kg) *log (x)*
Silt %	Silt %	K (cmol/kg) *log (x)*	Clay %
Resistance *log (x)*	Coarse sand %	Ca (cmol/kg) *log (x)*	Ca (cmol/kg) *log (x)*
Stone %	Stone %	NO_3 (N) *log (x)*	C %
Na (cmol/kg) *log (x)*		Fire intensity	T (cmol/kg) *log (x)*
CEC *log (x)*			
r_w:0.826	r_w:0.939	r_w:0.329	r_w:0.803

nutrients, fire and fire intensity were no longer important (due perhaps to the relief of the summer drought), while soil texture and Mg and Na levels were winter determinants. Evidently, autumn is the period where macronutrients are most important and the effects of fire on soil yeast population size seemingly disappears with periods of prolonged rainfall and/or low temperatures.

The observed mucoralean fungal distribution in November 2000 suggests the influence of fire and fire intensity. The rapid growth rates of the mucoralean fungi may explain the importance of macronutrient foodstuffs at an earlier time than observed for the soil yeasts (maximum correlation during November was not with fire intensity but with soil texture, P and K). Although total population sizes were still small in March 2001, the counts suggest an influence of fire intensity on mucoralean fungal population sizes. Assays from the burnt standing alien and burnt stacked alien sites exhibited smaller totals than unburnt standing aliens and burnt cleared areas. Macronutrient foodstuffs (coupled with resistance, soil texture and fire intensity) were, however, still the key determinants of mucoralean population size. No clear population size differences were measured in July 2001 and there were also no strong correlations with the environmental variables measured. Populations had however grown, coinciding with the advent of cooler, wetter conditions. Reasons for the large increases observed in burnt standing alien areas in September 2001 are speculative. It is possible that species turnover had occurred and that a specific group or species had benefitted from the post-fire conditions prevalent in the burnt standing alien area, while the species due to colonise the burnt stacked/ heat-scarred areas had all but disappeared, possibly as a consequence of superheating. In summary, indications are that macronutrients are important in early summer and the effects of fire on mucoralean fungal population size seemingly disappear with periods of prolonged rainfall and/or low temperatures. Population sizes also exhibit large fluctuations, possibly indicative of a more easily diffused group with associated patchy dispersal patterns (Ingold 1953).

Hymenomycetous fungal distributions in November 2000 suggested reduced population sizes in areas subjected to intense burning (standing and stacked aliens). Conversely, the March 2001 pattern (which was highly correlated with soil texture, CEC and Ca) suggested a negative association with fire and fire intensity. Hymeno- mycetes are, however, highly mobile, easily-dispersed orga- nisms and it is therefore possible that the observed patterns are indicative of patchy dispersal patterns (Ingold 1953). This may also explain the observed collapse in burnt standing alien areas in July 2001 while there were increases in other areas (coincident with the advent of winter). Alternatively, this collapse and the disappearance of hyme- nomycetes in the burnt stack samples in September 2001 may be an effect of superheating, eliminating a group due to colonise the heat scars at that time. Differences in environ- mental variable sets (showing maximum correlation with fungal populations within the study period) may also indicate a succession of different species or groups of species. Except for the elimination of hymenomycetous fungi in heat scars in September, alien plants and fire seem to have little effect on total populations of these fungi in soil.

Environmental variables were only strongly correlated with counts of total fungi (on MEA medium) in September 2001, when a combination of soil texture and nutrients were determinants. A possible explanation is that the environmental variables measured did not include those parameters most important in determining total fungal populations.

Table 8: Sets of environmental variables showing maximum harmonic (weighted Spearman) correlation (r_w) with the distributions of total heterotrophic micro-organisms enumerated on TSA in each of four assays

Summer 2000	Autumn 2001	Winter 2001	Spring 2001
Na %	Silt %	Mg %	P (mg/kg) *log (x)*
Fine sand %	Stone %	Clay %	Stone %
Medium sand %	Medium sand %	Ca (cmol/kg) *log (x)*	
H (cmol/kg)	H (cmol/kg) *log (x)*	C %	
	Coarse sand %		
	CEC *log (x)*		
r_w:0.734	r_w:0.847	r_w:0.828	r_w:0.800

Alternatively, the studied group (total fungi on MEA) could have been prohibitively diverse, clouding establishment of environmental determinants. Observed trends indicated that the highest total fungal counts were always from non-fynbos sites, with burnt non-fynbos areas having higher counts until September 2001 (spring). It is therefore possible that total fungal populations on (MEA medium) benefit from the presence of alien vegetation and the burning thereof.

Soil actinomycetes and other heterotrophic micro-organisms

The distribution of actinomycetes in November 2000 indicates that burning benefits populations at this stage. It may also be inferred that higher intensity burns are more beneficial since populations were appreciably larger in heat scars than in the burnt cleared areas immediately adjacent to them. Larger, albeit variable, population sizes in March 2001 denote that actinomycetes are able to reproduce and grow during the hot, dry summer months.

July 2001 showed larger actinomycete population sizes in all the samples except for unburnt fynbos. It is possible that the actinomycetes which showed such rapid population increases in unburnt fynbos soils by March 2001 and which had declined by July were different species than those present in the other areas, and had completed their life cycles earlier. An alternative hypothesis is that coinciding increases in population sizes of predatory soil amoebae account for decreases in actinomycetes in some areas (Alexander 1977, Paul and Clark 1996). It was also apparent in July that burnt non-fynbos areas had the highest counts (counts in burnt fynbos, unburnt fynbos and unburnt standing aliens being similar and lower) and that a combination of alien plant invasion and burning may benefit actinomycete population growth during the following winter. While actinomycete counts across the different areas sampled were highly variable, they all reacted to the advent of winter conditions. It is therefore probable that different species are dominant in the indigenous- and alien plant-dominated sites respectively and that they show variable responses to seasons, burning and soil environmental variables.

While clear patterns in the distributions of total heterotrophic organisms able to grow on TSA were not apparent, a similar pattern to that observed in actinomycete populations was obtained in March 2001, a possible manifestation of these counts. This pattern and the elevated levels in burnt stacked (heat-scarred) areas in June 2001 could possibly be explained by a different species or group of species benefitting from the post-fire environmental conditions present in unburnt fynbos and heat-scarred areas respectively. However, it must be taken into account that no single medium is nutritionally adequate for all the species present and the observed counts therefore only represent fractions of the total microbial population. Furthermore, the errors in sampling and sample preparation are frequently far greater than the inherent variations, and a single rootlet or particle of plant debris may be sufficient to change counts as much as 10- to 100-fold (Alexander 1977). The observed decreases in total heterotrophic microbial counts in unburnt fynbos and heat-scarred areas in July and September 2001 may, however, also have been a result of increased amoeboid activity following flushes of bacterial growth (Alexander 1977, Paul and Clark 1996). In conclusion, indications are that habitat modification (resulting from alien plant invasion and burning) on heterotrophic microbial populations benefits certain species or groups of species, but affects others negatively. This may explain the large variation between samples and between seasons.

This pilot study showed that woody alien plants, fire, fire intensity, season, soil texture and chemical characteristics together determine fungal, actinomycete and other heterotrophic microbial populations in the upper 0.10m of the soil profile. Current management of alien plant infestations have also been shown to influence certain microbial populations. Supplementary investigations (supported by soil chemical and molecular analyses) are warranted on particular species or taxa within the studied groups as well as on protozoa, to further elucidate the environmental effects of alien plants, fire and their management on soil microbial populations.

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